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RESEARCH ARTICLE

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Competitive drivers of interspecific deviations of crown morphology from theoretical predictions measured with Terrestrial Laser Scanning

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Abstract

1. Tree crown morphology is a key driver of forest dynamics, determining not only the competitiveness of an individual but also the competitive effect exerted on neighbouring trees. Multiple ecological theories, including metabolic scaling theory (MST), predict crown morphology from first principles, but typically lack consideration of competition. The accurate quantification of crown morphology to test theoretical predictions, and the canopy interactions that could alter them, has historically been limited by the simplicity and associated error of traditional crown measurements.
2. In this study, we calculate high-resolution two- and three-dimensional crown metrics from Terrestrial Laser Scanning data for 1,441 *Pinus sylvestris*, *P. nigra*, *Quercus faginea* and *Q. ilex* trees from a water-limited forest community in central Spain and test height-crown metric scaling relationships. We demonstrate new TLS methods to define symmetric and asymmetric neighbourhood metrics based on tree height, crown size and neighbour projected crown area, and test the importance of neighbourhood genus diversity on crown morphology by separating competition from congeneric and heterogeneric neighbours.
3. Competition negatively impacted all crown metrics except crown depth where only *P. nigra* showed sensitivity. Asymmetric competition was the strongest driver of pine crown morphology, but oaks were more sensitive to symmetric competition, in line with shade tolerance expectations. Congeneric competition reduced *Q. faginea* crown size and changed its shape, but we found no significant effects of heterogeneric neighbours. Most species and crown dimensions had height-crown scaling exponents below those predicted by MST, which may be due to water limitation effects. Pines and oaks showed large differences in crown depth to height scaling, with the former shallower and the latter deeper, in contrast to theoretical predictions.
4. *Synthesis*. Our study is the first to demonstrate the ability of TLS to characterise crown morphology from leaf-wood separated clouds and competitive neighbour effects in a water-limited forest community, and to use TLS metrics to test ecological crown scaling theory. Most crown metrics scaled below theoretical predictions. Pines were more sensitive to competition by larger neighbours and oaks

to crowding from all neighbours, with competition from neighbours of the same genus having a consistent negative effect.

KEYWORDS
crown morphology, forest ecology, metabolic scaling theory, plant–plant interactions, remote sensing, shade tolerance, Terrestrial Laser Scanning

1 | INTRODUCTION

The size and shape of tree crowns are first-order determinants of the light and microclimatic environment experienced by individuals, which drive growth, mortality and fecundity rates, and therefore whole-forest dynamics (Kobe et al., 1995; Pacala et al., 1996; Purves & Pacala, 2008). Accurate representation of tree allometry (how the dimensions of a tree change with size), is therefore an important consideration for predictive modelling frameworks (Fischer et al., 2019). Theories about the morphology of crowns, such as metabolic scaling theory (MST, West et al., 2009), provide an attractive approach to generalising allometric scaling, but testing their accuracy is challenging with traditional ground measured data, which typically require assumptions of uniformity of crown morphology to estimate properties such as area and volume (Liang et al., 2016; Ritter & Nothdurft, 2018). Terrestrial laser scanning (TLS) offers a novel method of quantifying tree morphology in high-resolution 3D detail (Disney, 2019), permitting testing of theoretical allometric relationships in detail never before possible.

Tree crown morphology is subject to multiple trade-offs, including lateral extension for light capture, maintenance of mechanical stability and hydraulic safety, and slow versus fast growth strategies (Verbeeck et al., 2019). MST, the most widely debated ecological scaling theory, does not directly consider these factors in crown allometry predictions, instead these play an ancillary role within the normalising constant. Others make simplified assumptions of crown morphology without accounting for evolutionary and environmental factors (such as sphere packing; Taubert et al., 2015). Similarly, competitive convergence points to community-wide shared architectural responses to physiological and environmental constraints (e.g. Iida et al., 2011; MacFarlane & Kane, 2017) as opposed to an ecological perspective where species, spatial and temporal niche and life history are favoured (e.g. Sapijanskas et al., 2014). MST infers allometric scaling from evolutionary optimisation principles (Enquist, 2002) and makes predictions of crown scaling through assumptions of elastic similarity (McMahon & Kronauer, 1976) and Euclidean-uniform crown shape (West et al., 2009). MST proposes that a tree is optimised for space filling, hydraulics efficiency and mechanical stability to reduce buckling risk. Some tests of MST using large datasets have found evidence against its generality, including its omission of competition for light (Coomes, 2006), and lack of consideration of abiotic effects including drought and cold (Lines et al., 2012; Olson et al., 2018) and ontogeny (Poorter et al., 2015). However, others have found supporting evidence (Enquist et al., 2009) and one recent tropical TLS study found branching exponents near MST but only for trees that were not water limited and were under direct light (Martin-Ducup et al., 2020). Traditional crown measurements taken with tape measures or rangefinders can only be used to estimate crown properties if assumptions about overall shape (e.g. that crowns are spherical, ellipsoidal or cylindrical) are made, limiting the extent to which scaling theories can be tested using such data.

The difficulty in accurately characterising tree crown morphology means that competition between trees is often quantified in similarly simplified ways, or even abstracted to the plot level using properties such as stem counts or basal area. Competition is often characterised as either asymmetric competition as competition for light and resources from larger individuals, or symmetric competition as competition from all surrounding individuals, including below ground factors (Potvin & Dutilleul, 2009; Pretzsch & Biber, 2010). Competition is known to influence tree shape, for example, asymmetric competition for light drives trees to extend vertically (Harja et al., 2012; Henry & Aarssen, 1999; Lines et al., 2012), often at the expense of crown expansion (Forrester et al., 2017). These allometric shifts have been found to align with species' shade tolerances, with less shade tolerant species responding more to shade cast by taller neighbours than to overall crowding (Coates et al., 2009, but see Bourdier et al., 2016). Neighbourhood diversity has been shown to have a positive effect on crown volume (Kunz et al., 2019), potentially driven by enhanced above-ground light capture due to structural and physiological differences (Jucker et al., 2015). For example, due to temporal differences in light capture (Jucker et al., 2014), or differing internal crown structure and arrangement leading to some crowns casting less shade than others (Ameztegui et al., 2012; Messier et al., 1998). Lack of diversity and associated similarity in function and niche occupation can lead to simpler homogenous canopies where mechanical canopy abrasion is high (Pretzsch, 2014; Putz et al., 1984). Within water-limited systems, tree-tree competition is further complicated by complex interactions below-ground between species with different rooting structures and acquisitive strategies (Grossiord, 2019; Grossiord et al., 2015). Under low soil water availability more drought tolerant species become more competitive, which can lead to reduced diversity effects (Grossiord et al., 2014; Jucker et al., 2014).

With both water limitation and competition for light present, Mediterranean forests represent an exciting environment to test theoretical allometric predictions and the competing trade-offs between crown expansion for light capture and the need to

minimise hydraulic risk from embolism in long branches (Smith et al., 2014; Verbeeck et al., 2019), as well as interacting asymmetric and symmetric competitive effects (Coates et al., 2009). Within these environments, shade can exert positive effects (Valladares et al., 2016), for example self-shading through adaptive crown shape and arrangement (Domingo et al., 2019; Pearcy et al., 2005) and shade cast by neighbours (Kothari et al., 2021) can reduce abiotic stresses. Horn (1971) hypothesises that crown depth is driven by both drought tolerance, increasing with aridity and shade tolerance, where conservative species minimise self-shading by reducing crown depth. Others argue that only shade tolerant species can maintain a positive carbon balance within lower self-shaded leaves (Poorter et al., 2012), leading to conflicting hypotheses when shade and drought tolerance rankings align. The significance of water limitation on tree allometry has been demonstrated in Iberian forests using simple ground-based measurements, with trees shorter and narrower in width under more severe drought (Lines et al., 2012). Now, new TLS methods allow us to analyse complex three-dimensional crown morphology within these ecosystems.

The ability of TLS to produce highly accurate measurements of a range of tree properties has been extensively demonstrated for tree mass (Calders et al., 2015), crown morphology (Kunz et al., 2019), leaf area (Calders et al., 2018), branching topology (Martin-Ducup et al., 2020), height (Liu et al., 2018) and stem diameter (Heinzel & Huber, 2018). In this study we present the first test of MST predictions of crown morphology scaling using Terrestrial Laser Scanning (existing studies have tested branching topology in the tropics: Lau et al., 2019; Martin-Ducup et al., 2020). We used 1,422 focal trees measured in central Spain to generate new neighbourhood competition indices and compared models of drivers of variation in crown morphology using a stepwise model comparison approach. Specifically, we tested four hypotheses: (**H1**) We hypothesise that there will be strong interspecific variation in height-crown scaling exponents and that these will fall below MST predictions, which may be due to water limitation in this system. Specifically, we expect crowns to be smaller in volume and narrower in lateral extent for a given height than predicted by MST, to reduce hydraulic path length (Olson et al., 2018; Ryan & Yoder, 1997) and total evaporative demand (Dawson, 1996) to minimise risk of embolism. (**H2**) We test whether crown depth varies with species' tolerance to abiotic stressors according to theoretical predictions, namely; whether drought intolerant species have deeper crowns to reduce direct exposure to radiation, and whether shade tolerant species have shallow crowns reflecting their conservative resource-use strategies (as hypothesised by Horn, 1971). (**H3**) We hypothesise that observed differences in scaling exponents between species will be explained by shade tolerance, and that asymmetric competition will drive crown morphology in less shade tolerant species, and with symmetric competition important for shade tolerant species. (**H4**) We hypothesise that congeneric-dominated neighbourhoods will have a negative impact on crown size and drive changes in crown shape through reduced complementarity in light use strategies (Fridley, 2012; Williams et al., 2017) and increased crown abrasion (Pretzsch, 2019).

2 | MATERIALS AND METHODS

2.1 | Field site and study design

We sampled 38 Mediterranean pine/oak 30 × 30 m forest plots in two areas of central Spain in July 2018 (Figure S1): 34 in Alto Tajo Natural Park, in Guadalajara province (40.9°N, 1.9°W), and four in Cuellar in Segovia province (41°N, 4°W). Plots in Alto Tajo (Jucker et al., 2014) form part of the wider FUNDIV project network, are situated at 960–1400 m a.s.l. and dominated by two pine (*Pinus sylvestris* and *Pinus nigra*) and two oak (*Quercus faginea* and *Quercus ilex*) species. *Pinus sylvestris* is the most shade intolerant species, followed by *P. nigra*, *Q. faginea* and finally *Q. ilex*. Drought tolerance follows the same ranking (Niinemets & Valladares, 2006; Puglielli et al., 2021). In total, there were 172 *P. sylvestris*, 338 *P. nigra*, 579 (132 multi-stem) *Q. faginea* and 173 (47 multi-stem) *Q. ilex* focal trees. The area is characterised by rugged topography and Mediterranean climate (mean annual temperature = 10.2°; mean annual precipitation = 499 mm/year). Plots in Cuellar (Madrigal-González et al., 2017) are situated at 841 m a.s.l. and is dominated by *P. pinaster*, with *P. sylvestris* in riparian zones. The terrain is flat and climate Mediterranean (mean annual temperature = 11.9°; mean annual precipitation = 430 mm/year).

2.2 | TLS data collection and initial processing

We scanned plots using a Leica HDS6200 scanner, using a square grid system of 16 scans spaced at 10 m, (Wilkes et al., 2017). We used a scanner resolution set to 3.1 mm and spherical targets to enable scans to be combined to create whole-plot point clouds. Scans were co-registered using Leica's propriety Cyclone software, and xyz coordinate data were exported. Using tools from the Point Cloud Library (PCL), we cut plot clouds with a 7.5m horizontal buffer to the plot boundary, filtered using height-dependent statistical filtering to minimise information loss in the upper areas of the canopy where returns were less dense, and downsampled to 5 cm to reduce computational time. Trees were automatically identified and segmented from the whole-plot cloud using the treeseg package (Burt et al., 2019), followed by manual refinement to ensure all canopy trees were identified and represented correctly (Calders et al., 2020). Individual tree point clouds were processed to separate leaf and wood material using the TLSeparation python library (Vicari et al., 2019). Stem maps recorded in the field, created using a 10 m grid within our plot, were used to determine species of each tree in each point cloud. Multi-stem trees were identified automatically as stems that bifurcated below 1.3 m, and results were visually verified and corrected where necessary.

2.3 | Characterisation of tree crown morphology from TLS data

We computed crown metrics for each target tree using the leaf cloud, with the lowest (by vertical height) 3% of points removed to avoid errors due to inaccurate classification, returns from re-sprouts or otherwise spurious foliage. This approach avoided using the common first primary branch as a determinant of crown depth, which can lead to interspecific biases in estimation due to pines often having multiple dead lower branches (Schoonmaker et al., 2014). We characterised crown morphology using a concave hull approach in both 2D and 3D (Figure 1) and used this to calculate our six crown metrics: radius, projected area, depth, surface area, volume and crown depth-to-diameter ratio (hereafter termed 'relative depth'). For multi-stemmed individuals we fit hulls to all stems' crowns together and treated these individuals separately within statistical analyses. All metrics were calculated using the Point Cloud Library (PCL) and R (R Core Development Team). Crown volume and surface area were calculated using a 3D concave hull fit as opposed to convex (Figure S2), to the leaf point cloud using the alphashape3D package in R (Lafarge & Pateiro-Lopez, 2017) with alpha (tightness of fit parameter) set to 0.3 (Figure 1a). Crown radius and 2D projected area were calculated using the concaveman package in R (Gombin et al., 2020) with alpha set to 2 (Figure 1b), which is higher to reduce computational time and deemed appropriate visually. The mean distance of all hull vertices (points on the edge of the hull) to the centroid was used to calculate crown radius. To derive crown depth, we subtracted the minimum of the leaf cloud z-axis from height. We calculated tree height using the extent of the whole tree cloud along the z-axis, and relative depth was calculated as crown width (radius multiplied by 2) divided by crown depth. Given the low stem bifurcation point, irregularity in shape and occlusion near the stem base due to shrubs, reliable DBH estimates are hard to extract for all trees in this system. We adapted the approach within treeseg (Burt et al., 2019) to extract sections of the trunk at a higher resolution (1 cm) from the original point cloud to provide more space to fit cylinders. Each section was sliced three ways and cylinders detected within each slice. This not only helped locate sections of cylindrical shape along sinuous stems but also provided an automated means to detect multi-stems. Only stems with high stability had DBH values ($N = 972$; 77% of total single stems). Distributions of all crown metrics can be found in Supporting Information (Figure S3).

2.4 | MST predictions

Metabolic scaling theory crown predictions assume elastic similarity scaling (with exponent = 2/3) of tree height with stem diameter (McMahon & Kronauer, 1976) and isometric (i.e. linear) scaling (exponent = 1) between tree height and crown radius and depth. We tested exponents for height-crown rather than diameter at breast height (DBH)-crown scaling due to the below canopy complexity within our study system (e.g. multi-stemmed trees and occlusion) which affected accurate DBH retrieval. Both height and DBH are predicted directly from mass in MST (West et al., 1999), with convention choosing DBH due to ease of measurement in the field but in the future height is most likely to become more relevant with the emerge of remote sensing technologies. Our use of height instead does not affect our ability to test the predictions of MST crown scaling, but we do present height-diameter exponents in Figure S4 for a subset of the data where DBH was extractable and robust. MST predicted exponents for height-crown scaling are: 3 for crown volume, 2 for crown surface area and projected area, 1 for crown radius

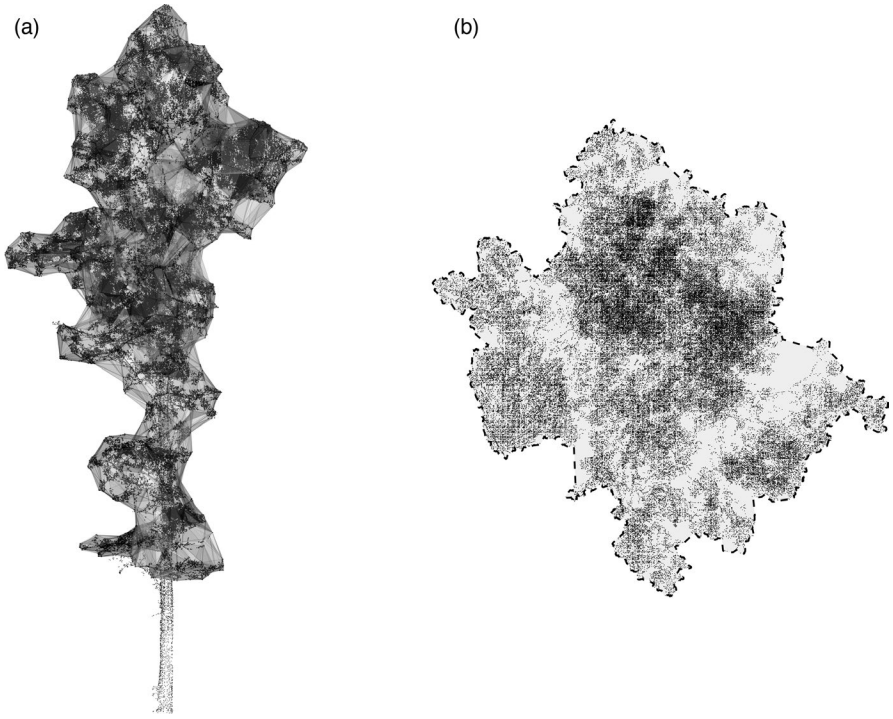

FIGURE 1 Example of TLS data processing and crown metric calculation. (a) TLS point cloud of a *Quercusfaginea* in Alto Tajo, showing the leaf point cloud wrapped in a 3D concave hull. (b) Top-down view of the same tree (leaf cloud only), showing crown projected area calculation using a 2D concave hull. 2D and 3D hulls were used to calculate metrics of crown radius (mean), diameter, projected area, depth, surface area, volume and relative depth. Whole-tree point clouds were used to calculate tree height

and depth and 0 (no relationship) for crown relative depth (the ratio of crown depth to crown width (West et al., 2009).

2.5 | TLS-derived competitive neighbourhood metrics

We used the TLS point clouds to define measures of neighbourhood interaction based on nearby trees' crown area. We define a target tree's competitive neighbourhood as a circular neighbourhood centred on the centroid of the target tree's crown and with diameter twice the maximum crown diameter of the target tree (Figure 2), with a minimum neighbourhood of 5 m diameter (due to possible poor performance at smaller diameters, Fraver et al., 2014). Our neighbourhood distance criteria are towards the smaller end of the range within the literature (Bella, 1971; Berger & Hildenbrandt, 2003; Fraver et al., 2014; Grote et al., 2020; Lorimer, 1983; Pretzsch & Biber, 2010), but was chosen to avoid known steep declines of competition with distance (Thorpe et al., 2010). We define competition for a focal tree as the canopy cover within the neighbourhood from other trees (crown area index, allowing values >1; Figure 2). Focal trees with a neighbourhood intersecting the plot perimeter were excluded but included as neighbouring trees for other focal individuals (see Table S1 for sample sizes). We captured competition from all trees ('symmetric competition', Figure 2a), from taller trees only ('asymmetric competition', Figure 2b), and genus-specific competition from all trees ('gegenus level symmetric competition', Figure 2c) and from taller trees only ('gegenus level asymmetric competition', Figure 2d). Symmetric competition was calculated as the sum of all crown projected area within the circular neighbourhood, divided by the area of the neighbourhood circle (crown area index, CAI, Figure 2a). Asymmetric competition was calculated using only the canopy projected area of the taller individuals (height >90% focal tree height) within each neighbourhood (Figure 2b). Similar thresholds to define asymmetric competition have been applied in other studies (e.g. Coomes et al., 2014). Genus-specific symmetric and asymmetric competition are calculated as CAI for each genus within the neighbourhood, with heterogeneric competition from trees of the opposite genus and congeneric from trees of the same genus as the target tree (Figure 2c,d). Distributions of all neighbourhood metrics can be found in Supporting Information (Figure S5).

2.6 | Statistical estimation of scaling exponents and competitive effects

We fit height-crown metric relationships and tested the importance of neighbourhood competition using log-transformed data using linear mixed models (LMMs) within the lme4 package in R (Bates et al., 2015). We fit models separately for each species, and we separated multi-stemmed individuals (present for oak species only) and performed separate analyses on them as they are likely to show distinct scaling properties to single-stemmed individuals of the same species. Only the exponents will be presented for multi-stems. We tested models of increasing complexity (described below), comparing at each step to find the best model for each species using the Akaike information criterion (AIC; see Tables S2 and S3 for full AIC model comparison).

For each species (or multi-stem group) *s*, we first determined whether height-crown scaling for individual *i* varies between plots (*j*), by testing the inclusion of an intercept only random plot effect:

$$\log\left(\mathrm{CM}_i\right) = a_s + b_s \log H_i + c_s \,\mathrm{Site}_i, \tag{1}$$

$$\log\left(\mathrm{CM}_i\right) = a_s + b_s \log H_i + c_s \,\mathrm{Site}_i + \mathrm{Plot}_{s,j}, \tag{2}$$

where H_i is the height of the stem; Site_i, the blocking factor to account for variability between sites; a_s, b_s and c_s are parameters to be fit; CM represents each of our six crown metrics and $\mathrm{Plot}_{s,j}$ is the random plot effect, (all parameters are species/multi-stem group specific).

Next, we determined which mode of neighbourhood competition metric (NM: either symmetric or asymmetric) was most important for each crown metric, by adding each in turn to the chosen model from the previous step (either Equations 1 or 2):

$$\log\left(\mathrm{CM}_i\right) = a_s + b_s \log H_i + c_s \,\mathrm{Site}_i + d_s \mathrm{NM}_i, \tag{3}$$

$$\log\left(\mathrm{CM}_i\right) = a_s + b_s \log H_i + c_s \mathrm{Site}_i + d_s \mathrm{NM}_i + \mathrm{Plot}_{s,j}, \tag{4}$$

where NM_i is either asymmetric or symmetric neighbourhood competition, without (Equation 3) or with (Equation 4) a random plot effect (a_s, b_s, c_s and d_s are parameters to be fit, Site_i a blocking factor to account for variability between sites and $\mathrm{Plot}_{s,j}$ a random plot effect). Lastly, if the best model included either symmetric or asymmetric competition, we tested further models that split the selected competition type into two genus-specific components (separate congeneric and heterogeneric competition, either asymmetric or symmetric depending on the previous step):

$$\log\left(\mathrm{CM}_i\right) = a_s + b_s \log H_i + c_s \,\mathrm{Site}_i + d_s \mathrm{CON}_i + e_s \,\mathrm{HET}_i, \tag{5}$$

$$\log\left(\mathrm{CM}_i\right) = a_s + b_s \log H_i + c_s \,\mathit{Site}_i + d_s \,\mathrm{CON}_i + e_s \,\mathrm{HET}_i + \mathrm{Plot}_{s,j}, \tag{6}$$

where CON_i and HET_i are congeneric and heterogeneric asymmetric or symmetric competition; a_s, b_s, c_s, d_s and e_s are species-specific parameters to be fit; Site_i, the blocking factor to account for variability between sites and $\mathrm{Plot}_{s,j}$ is the random plot effect. We also tested whether the magnitude of the random effect is statistically different across two groups (mono genus and mixed genus) at the plot scale.

We also fit scaling exponent results using standardised major axis (SMA) using the R package smatr (Warton et al., 2012). SMA is often used for allometric scaling when there is no clear relationship between two variables and the objective is to simply estimate the intercept and slope of the line (Smith, 2009), but is less flexible than LMMs as random effects (e.g. plot effect) cannot be included. Results were consistent across methods, with the exception of crown relative depth where although both methods showed a negative relationship, the slope for SMA was steeper than for

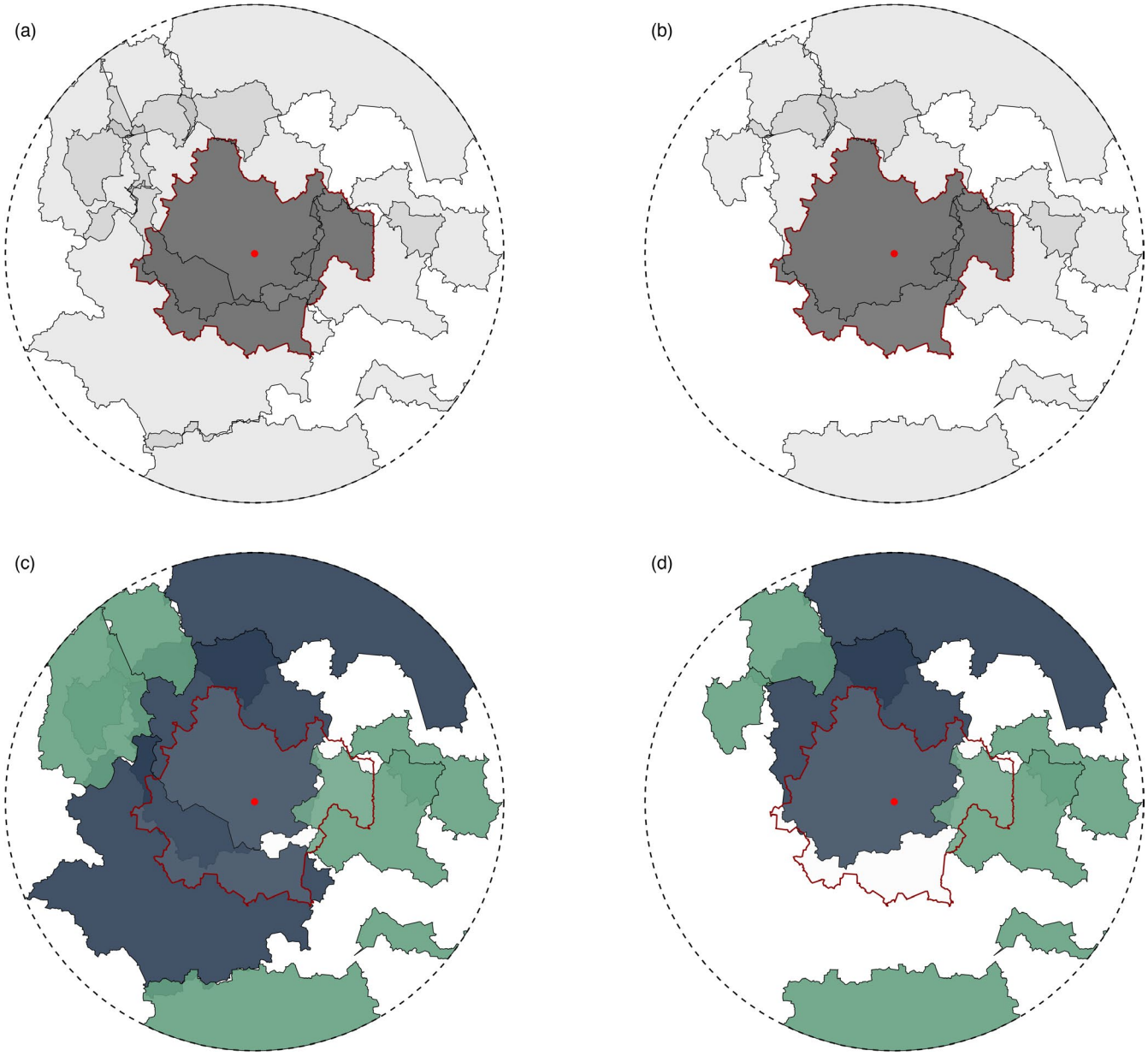

FIGURE 2 Example TLS-derived neighbourhood competition metrics. Nadir view of a *Quercusfaginea* tree crown from Alto Tajo, Spain, showing; (a) asymmetric, (b) symmetric, (c) symmetric congeneric and heterogeneric and (d) asymmetric congeneric and heterogeneric neighbourhood competition metrics of the tree. Dashed circles represent the neighbourhood (defined as twice focal trees' maximum crown diameter). Red dots show the focal crown centroid and neighbourhood centre, and red line the focal crown edge. (a) and (b), The focal crown is shown in dark grey and neighbouring trees in light grey. (c and d), The focal tree crown is shown in outline only, surrounded by pines (here, heterogeneric) in blue and oaks (here, congeneric) in green

LMM results suggesting a weak relationship and lack of robustness (Warton et al., 2006; Table 1; Tables S4 and S5).

3 | RESULTS

3.1 | Competitive and plot effects were evident for all species

Model comparison identified competitive effects to be important for most metrics and species (Table 1). Scaling within multi-stemmed trees was highly variable, with large error bars on estimates of the exponent, and for some metrics multi-stems showed substantial deviation from their single-stemmed individuals of the same species. These groups also had lower sample sizes (Table S1); therefore, we present results for multi-stem scaling exponents but not their competitive effects. Crown depth was the only metric to show insensitivity to competition, except *P. nigra*, with tree height the only selected predictor and crown relative depth the only metric where plot effects were not in the final model, but this was for the pines only. All other metrics selected for models including a random plot effect, that accounted for variability between plots not captured in other explanatory variables.

TABLE 1 Model selection results showing the strongest neighbourhood competition metric drivers of height-crown scaling variation. AIC comparison of LMM model results of single-stems only, comparing candidate models including asymmetric, symmetric and heterogeneric/congeneric neighbourhood metrics as explanatory variables (Equations 1–6). Species are ordered according to their shade tolerance. Results where either Equations 1 or 2 were selected are not displayed in the table. Estimates for the coefficient (c and d in Equations 3–6) of the most important competitive metrics are shown for each variable and species (single-stemmed individuals). Delta AIC results for all models are available within Supporting Information (Table S2)

Crown metric	Term[a]	Coefficient	95% CI	Random effect (*SD*)
log(crown volume)				
P. sylvestris	Asymmetric competition	−0.64***	(−0.44, −0.77)	0.87
P. nigra	Asymmetric competition	−0.65***	(−0.58, −0.71)	0.36
Q. faginea	Symmetric congeneric	−0.46***	(−0.34, −0.56)	0.33
Q. faginea	Symmetric heterogeneric	−0.19	(0.11, −0.4)	0.33
Q. ilex	Symmetric competition	−0.67***	(−0.44, −0.8)	0.32
log(crown surface area)				
P. sylvestris	Asymmetric competition	−0.56***	(−0.39, −0.68)	0.97
P. nigra	Asymmetric competition	−0.58***	(−0.5, −0.65)	0.35
Q. faginea	Symmetric congeneric	−0.34***	(−0.23, −0.44)	0.27
Q. faginea	Symmetric heterogeneric	−0.13	(0.12, −0.3)	0.27
Q. ilex	Symmetric competition	−0.42**	(−0.14, −0.6)	0.24
log(crown projected area)				
P. sylvestris	Asymmetric competition	−0.54***	(−0.37, −0.67)	0.56
P. nigra	Asymmetric competition	−0.59***	(−0.51, −0.65)	0.31
Q. faginea	Symmetric congeneric	−0.33***	(−0.21, −0.44)	0.33
Q. faginea	Symmetric heterogeneric	−0.08	(0.19, −0.3)	0.33
Q. ilex	Symmetric competition	−0.43**	(−0.12, −0.63)	0.26
log(crown radius)				
P. sylvestris	Asymmetric competition	−0.32***	(−0.2, −0.41)	0.24
P. nigra	Asymmetric competition	−0.36***	(−0.3, −0.41)	0.15
Q. faginea	Symmetric congeneric	−0.18***	(−0.1, −0.24)	0.14
Q. faginea	Symmetric heterogeneric	−0.04	(0.1, −0.16)	0.14
Q. ilex	Symmetric competition	−0.22*	(−0.03, −0.37)	0.13
log(crown depth)				
P. nigra	Symmetric competition	−0.15**	(−0.04, −0.25)	0.14
log(crown relative depth)				
P. sylvestris	Asymmetric competition	−0.36***	(−0.18, −0.49)	—
P. nigra	Asymmetric competition	−0.15**	(−0.03, −0.25)	—
Q. fagineas	Symmetric congeneric	−0.2***	(−0.11, −0.27)	0.17
Q. faginea	Symmetric heterogeneric	−0.03	(0.13, −0.17)	0.17

[a]AIC ≤ 2.

*$p \leq 0.05$, **$p \leq 0.01$, ***$p \leq 0.001$.

The random plot effect variation was consistently higher for the pines than for oaks, with *P. sylvestris* showing the strongest variability across plots for all metrics (see Table 1). Our results also highlight how misrepresentations of tree morphology and competition can arise from traditional ground data by overlooking the complex shapes, spatial configurations and plasticity that trees adopt to fill space as well as their clustering (see Figures S6 and S7).

3.2 | Crown scaling exponents were below MST prediction for most species and metrics

We compared scaling exponents (b in Equations 1–6) for the best fit model for each species and metric (Table 1) with those predicted by MST. We found that height-crown scaling relationships were highly variable between species, and within a species multi-stemmed individual showed higher variation than single-stemmed equivalents (Figure 3). Most, but not all, height-crown scaling relationships were at or lower than MST predictions, supporting our hypothesis (**H1**). Our results were also supported by SMA analyses (Table S3) and evidenced interspecifically (Table S4). Crown volume scaling exponents for all species were significantly smaller than predicted by MST (Figure 3a), despite our models including both competitive and plot effects. Crown surface area exponent estimates overlapped MST predictions for *P. sylvestris* and *Q. ilex* but were lower for *P. nigra* and *Q. faginea* (Figure 3b). For exponents estimated from the 2D hull, most are significantly below those predicted by MST, although *Q. ilex* and

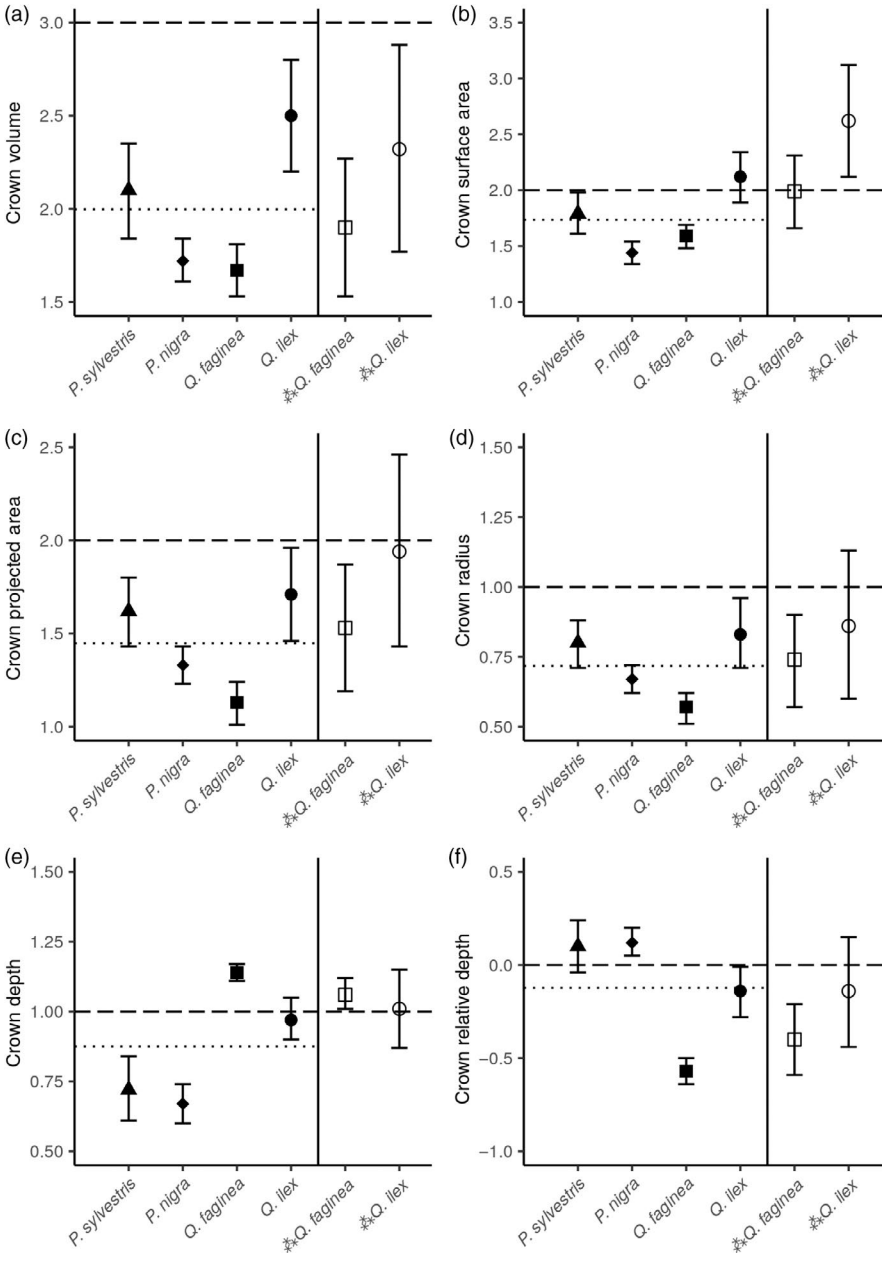

FIGURE 3 LMM-derived exponents of crown-height relationships for (a) crown volume; (b) crown surface area; (c) crown projected area; (d) crown radius; (e) crown depth and (f) crown relative depth (b in Equations 1–6) from the best model for each species, selected using AIC (Table 1). Error bars represent 95% confidence intervals. Exponents are shown for all species' single-stem data, with multi-stem individuals' relationships were fit separately (oak species only), separated by the solid vertical black line. Species are ordered according to shade tolerance (Niinemets & Valladares, 2006; Puglielli et al., 2021), increasing left to right. MST predictions are shown by the horizontal dashed line while the dotted is the average of the four single-stem exponents (single-stem data only, left of solid black line)

P. sylvestris nearer of the four species (Figure 3c,d). Inter-genus differences in scaling exponents were particularly striking for crown depth and relative depth (Figure 3e,f), with this difference in relative depth even more pronounced using the SMA approach (see Table S3). *Pinus sylvestris* had higher exponents for all metrics than *P. nigra*, and *Q. faginea* had lower than *Q. ilex* for all but crown depth scaling. *P. nigra* and *Q. faginea* had exponents closer to one another than to species of the same genus and lower for all but depth and relative depth, while both oaks had exponents that never overlapped for all metrics. For the diameter–height scaling conducted on a subset of the data, we found pines to scale at MST and therefore, elastic similarity, and both oaks below MST.

Crown depth scaled nonlinearly with height for three out of four species, in contrast to MST predictions. Oaks and pines showed distinct crown scaling with height in the opposite direction to our second hypothesis (**H2**); both oak species had deeper crowns for a given height than MST predictions, and both pine species had shallower (Figure 3e). MST predicts no relationship between relative depth and tree height but here we find not only height dependence, but also differences between genera, with oaks showing smaller and pines larger relative crown depths, with increasing height (Figure 3f).

3.3 | Shade tolerance explained interspecific differences in sensitivity to competition type

Using model comparison (Table 1) we found that, across all crown metric scaling relationships, competition negatively affected crown

size and changed crown shape. The most important competitive effects were asymmetric for *P. sylvestris* and *P. nigra* and symmetric for *Q. faginea* and *Q. ilex*, in support of our hypothesis that shade tolerance determines the most important competitive effects (**H3**), since these pines are less shade tolerant than the oaks. *P. nigra* was the only species to show crown depth sensitivity to competition, with decreasing depth with increasing symmetric competition, which is notably in contrast to the sensitivity to asymmetric competition for its other metrics. Relative depth was negatively affected by competition for all species except *Q. ilex*, with crowns narrower relative to height with increasing competition and the effects asymmetric for *P. sylvestris* and *P. nigra* and symmetric for *Q. ilex*. Symmetric competition rather than asymmetric was most important in positively effecting both pines and *Q. ilex* tree height, whereas asymmetric neighbours had negative effects on *Q. faginea* height. All but *Q. faginea* rejected models that split neighbourhood metrics into gegenus level. Even when selected, heterogeneric effects were negligible, with confidence intervals consistently spanning zero, while congeneric effects were consistently negative. Across data, most heterogeneric neighbourhood values were very low (see distributions in Figure S5). Post-hoc analyses on the random effect showed limited evidence of plot-level diversity effects; only two metrics (crown surface area and depth) of two species (*P. nigra* and *Q. faginea)* had statistically significant differences ($p < 0.05$) between mono genus and mixed genus plots.

4 | DISCUSSION

4.1 | Crown metrics scaled below MST predictions

Almost all species' crown metrics were smaller for a given height than predicted by MST (Figure 2). These results agree with findings using simple ground-based measurements from regional forest inventory data (Lines et al., 2012; Olson et al., 2018), and provides further evidence for the role of external factors in determining complex crown morphology, and the power of TLS to reveal these. These findings were consistent whether species were considered separately or together (Table 1; Table S3). In addition, the significance of plot effects of many species suggests additional abiotic drivers (e.g. exposure, aspect, topographic wetness index) not captured by our analyses (Jucker et al., 2018; Muscarella et al., 2020). We found little evidence that our plot effect is capturing residual genus diversity affects, with statistical differences in its magnitude across mono and mixed genus plots only significant for two species (*P. nigra* and *Q. faginea*) and two metrics (crown surface area and crown depth). Nutrient richness has also likely impacts on tree allometry (e.g. Urban et al., 2013) but this information was not available across our sites but a strong protocol was deployed to minimise these differences (Baeten et al., 2013). In this water-limited ecosystem, individuals may increase crown size at a slower rate due to higher allocation to below-ground than above-ground organs (Ledo et al., 2018), and due to the need for crowns to function within a safer hydraulic margin, necessitating reduced hydraulic path lengths (Poorter et al., 2012; Smith et al., 2014). Negative relationships between crown dimensions and precipitation have also been found across continents (Loubota Panzou et al., 2021).

Despite the fact that all species' volumes scaled below MST predictions, several one- and two-dimensional metrics scaled at or above MST, demonstrating the value of three-dimensional data to provide a robust test of crown morphological theoretical predictions. For example, in this study, *Q. faginea* scaled above MST for crown depth but below for crown projected area, radius and volume. Pretzsch and Dieler (2012) also found different crown metric scaling exponents to be above and below MST within the same species. All species had lower crown radius scaling exponents than MST, with water limitation one possible explanation (Dai et al., 2009; Lines et al., 2012). Narrower crowns could also be caused by higher wind exposure in taller trees (Loehle, 2016), which can be evident even when under hydraulic stress (Niez et al., 2019), but there is also evidence of larger crowns in areas of increasing wind speed (Loubota Panzou et al., 2021). Crown radius to height scaling is a core assumption for scaling from individual canopy and stand level space filling predictions in MST (West et al., 2009). However, our results highlight that lateral extension of tree crowns is reduced by both asymmetric and symmetric competition, and even when this was accounted for, exponents fell below MST. Given that trees respond to reduced water availability through reductions in height, and therefore path length (Olson et al., 2018), increased hydraulic safety may emerge through reduced lateral path length (Smith et al., 2014). In fact, trees under stress often shed terminal branches (McDowell et al., 2008; Rood et al., 2000), with remaining branches shorter in path length (Olson et al., 2018), lowering the risk of embolism. Within homogenously structured stands, crown abrasion through wind sway is also likely to spatially restrict lateral expansion (Meng et al., 2006). The multi-stemmed individuals had scaling relationships with much higher variation (Figure 3), highlighting the need for separate allometric approaches for re-sprouting multi-stemmed trees (Matula et al., 2015).

We found high variability in crown volume scaling between species but known drought tolerances mostly fail to explain these differences. *Quercus ilex* had the highest volume and projected area scaling exponents, suggesting its extensive root systems and drought tolerance may relieve hydraulic constraints on crown expansion (David et al., 2007; Forner, Valladares, Aranda, 2018). However, the next largest exponents were *P. sylvestris*, which is at its southernmost part of its range and its physiological limits (Castro et al., 2004), as well as being the least drought tolerant species in our study, with rooting mostly confined to shallow soil layers (Irvine et al., 1998). In this dataset, many *P. sylvestris* stems are in riparian sites in Cuellar, affording greater access to water reserves (McDowell et al., 2019) and allowing crowns to expand without risking hydraulic failure (Dawson, 1996). Trees at this site were also able to extend more in height for a given DBH (see Table S5), suggesting greater availability of water is alleviating limits to height posed by hydraulics (Ryan & Yoder, 1997). This still fails to explain the relatively wider CIs and higher *SD* in plot effects for this species (Figure 1; Table 1), and mostly higher scaling exponents compared

to *P. nigra*, because site was included as a blocking factor within each model. Although *P. sylvestris* is less drought tolerant than *P. nigra* (Grossiord et al., 2015; Niinemets & Valladares, 2006), height–diameter allometry is thought to have been driven by distinct historical and climate constraints (Vizcaíno-Palomar et al., 2016) and offers a possible explanation to this divergent pattern. The differences between scaling exponents for oaks, with *Q. faginea* generally lower than *Q. ilex* (Figure 3), may reflect differences in these species' responses to water limitation. For example, studies have found reduced bud development (Montserrat-Martí et al., 2009) and basal-area growth (Granda et al., 2013) in *Q. faginea* compared to *Q. ilex* with increasing drought. The height-DBH exponent was identical between the two species (see Figure S4) with both showing a shorter stature compared to both pines, providing greater safety from embolism (Fajardo et al., 2019). Despite *Q. faginea* having deep rooting and capacity to maintain open stomata during drought (Cochard et al., 1996), it is more sensitive to edaphic conditions (Alonso-Forn et al., 2021). In addition, *Q. ilex* remains more photosynthetically active during summer months (Montserrat-Martí et al., 2009) with greater radial root expansion (Alday et al., 2020) and more fine roots than *Q. faginea* (Coll et al., 2012).

In this study we found minimal difference between *Q. faginea* and *P. nigra* for crown volume scaling. However, for a similar volume–height scaling exponent, *P. nigra* crowns have smaller crown depth but larger radius and therefore high relative depth, whereas the opposite was true for *Q. faginea*. The shape adopted by *Q. faginea* is presumed to be the more hydraulically efficient form (Smith et al., 2014) but also associated with higher self-shading (Pearcy et al., 2005) which may limit its emergence to shade tolerant species, as evidenced by *Q. faginea*. Shade tolerance may also explain the difference in surface area scaling between both *P. nigra* and *Q. faginea*, with a larger value reflecting a higher degree of penetrating cavities, indicative of more foliage in the interior of the crown (Osawa, 1995). *Quercus faginea* may have greater drought tolerance than *P. nigra* (Forner, Valladares, Aranda, 2018) but some evidence suggests the latter is potentially more competitive in the long run (Forner, Valladares, Bonal, et al., 2018) and has deep roots enabling similar deep-water exploitation (Peñuelas & Filella, 2003).

4.2 | Sensitivity to competition type is driven by shade tolerance

Species' shade tolerance was a key determinant of whether asymmetric or symmetric competition was more important. Both pines' crown metrics were consistently negatively affected by asymmetric competition, suggesting shading by neighbours is an important determinant of crown morphology. Others have highlighted the significance of light limitation in driving pine dynamics (Bravo-Oviedo et al., 2006; Martin-Benito et al., 2011), and our findings align with findings of smaller crown projected area (Dieler & Pretzsch, 2013; Lines et al., 2012; Thorpe et al., 2010) and crown radius (del Río et al., 2019), but contrast (Harja et al., 2012), who found minimal sensitivity in volume or lateral extent to light availability. The observed effect of asymmetric competition on crown morphology suggests a greater investment in height growth than branching with apical dominance, which is typical of shade intolerant conifer species (Carnicer et al., 2013; Poorter et al., 2012; Valladares & Niinemets, 2008), and aggravated in dense stands (Henry & Aarssen, 1999). In fact, analysis of height-DBH allometry found symmetric rather than asymmetric competition, which was predominant for all other metrics, to drive height extension (see Table S5) and therefore vertically confront neighbours in attempt to overtop (Gruntman et al., 2017). The shift in allocation away from crown expansion when prioritising height not only improves mechanical stability but also reduces hydraulic embolism risk, since large crowns necessitate a large stem xylem cross-sectional area (Shinozaki et al., 1964), which is often compromised with height extension (MacFarlane & Kane, 2017). Although stability against wind may drive crown morphology (Loehle, 2016), the proximity of trees in more competitive neighbourhoods lessens tree sway (Brüchert & Gardiner, 2006), reducing buckling risk.

The consistent negative effect of symmetric competition on oak crown metrics suggests that below-ground factors may be more important in determining crown morphology for oaks than for pines, in line with expectations based on shade tolerance (Coates et al., 2009). Although both oaks had similar height-DBH exponents, they showed distinct impacts of competition on height, with *Q. faginea* shorter with increasing asymmetric competition and *Q. ilex* showing the opposite response (see Table S5). Jucker et al., (2014) found pines to be shorter and oaks taller when mixed with the opposite genus at the plot scale, but we found no such effects at the neighbourhood scale. Errors in height measurements using traditional techniques may be more sensitive to stand structure and species than those from TLS (Wang et al., 2019).

Quercus ilex root systems are dimorphic with the dependence on deeper roots increasing during summer (Barbeta et al., 2015; Cubera & Moreno, 2007; Joffre & Rambal, 1993; Moreno & Cubera, 2008). Morán-López et al. (2016) and Forner et al. (2020) both found positive hydraulic response in *Q. ilex* with increasing fragmentation, suggesting that crown size (volume) is mediated by the ability of its extensive root system to exploit inter-tree space for water. Defoliation during drought in this species also suggests that deep roots do not always equate to insensitivity to water limitation (Corcuera et al., 2004) with topography one possible factor that could restrict access (Fan et al., 2017). Sensitivity to symmetric competition by *Q. faginea* is likely associated with it functioning near threshold tolerance in this landscape (Forner et al., 2014) and its dependence on a reliable water supply (Castro-Díez et al., 1997), evidenced by defoliation events during drought (Corcuera et al., 2004).

4.3 | Neighbourhood genus diversity effects on crown morphology

For most species, models selected for total competitive effects, with separate congeneric and heterogeneric effects only important for *Q.*

faginea. Neighbourhood genus diversity had consistent effects on *Q. faginea*, by reducing crown size and changing crown shape, whereas all other species selected for models containing only total competitive effects for all crown metrics. Post-hoc tests showed little evidence for genus diversity effects at a plot level; genus diversity was only important for two metrics (crown surface area and crown depth) for two species; *Q. faginea* and *P. nigra*. Our results for both pine species are in agreement with other studies which found the same species to be primarily sensitive to total competition over mixing effects (Condés et al., 2020). The consistent negative effects of congenerics on *Q. faginea* highlight that, for this species, competition is most intense among neighbourhoods containing the same genus, in agreement with findings at the species level (Kunstler et al., 2016) and suggesting resource partitioning (Gómez-Aparicio et al., 2011; Tilman, 1982; Uriarte et al., 2004). This may also suggest a positive effect of shallow-rooted heterogenerics such as *P. sylvestris* within its neighbourhood, as is observed in our study sites (Grossiord et al., 2015). *Quercus ilex*, which in contrast to *Q. faginea* was sensitive to total competition, is not found with *P. sylvestris* within its neighbourhood in our study sites but is found with *P. nigra* which is able to grow deep roots and therefore compete below-ground (Grossiord et al., 2015; Peñuelas & Filella, 2003). When neighboured by more shallow rooted species such as *P. halepensis*, there is evidence that *Q. ilex* grows deeper roots, increasing spatial complementarity in water extraction (del Castillo et al., 2016; Sardans et al., 2004). Without these trait differences, *Q. ilex* may be confined to shallower depths, where competition for water is greatest (Craine & Dybzinski, 2013).

Although our study did not identify positive heterogeneric effects at the neighbourhood scale, post-hoc analyses on the plot effect showed that for two metrics and two species, plot-level genus diversity may alter crown plasticity. In contrast to our findings, Jucker et al., (2014) found consistent positive plot diversity effects on pine and oak crown volume. This may be due to the difference in how volume is estimated by ground methods that rely on two-dimensional measures (radius and depth) versus using our 3D point clouds. However, we found no evidence of a plot genus diversity effect on measures of crown lateral extent or volume for any of our study species. Within water-limited forest communities, interactions are dynamic and depend on many abiotic factors and can easily shift from positive to negative (Holmgren et al., 1997) making the identification of clear drivers using a single field campaign difficult.

4.4 | Shade not drought tolerance determines crown depth

We found that shade tolerant species had deeper crowns than shade intolerant species, in agreement with Poorter et al. (2012) and Ackerly (1999) who propose that leaves and branches are abscised once they become a net carbon drain. Shade and drought tolerance rankings are the same for our study species, meaning that we found no evidence that drought intolerant species had deeper crowns to self-shade and reduce radiation stress (as hypothesised by Domingo et al., 2019; Pearcy et al., 2005), and indeed we found no effect of neighbourhood competition—which would increase shading and therefore reduce radiation stress—on depth for most species. The more drought sensitive pines had shallower crowns for a given height and the shade tolerant oaks deeper, with the former below and the latter at or above MST scaling predictions. *Q. ilex* was the only species to scale isometrically with tree height, as predicted by MST, whereas *Q. faginea* had crown depth–height scaling exponent greater than one. Confidence intervals for exponents were narrow, and plot-plot variability low, for all species. This suggests that height is a strong predictor of crown depth, in agreement with a global analysis (Shenkin et al., 2020). That study found an exponent of 2/3, which is close to our result for pines but much lower than that of our oaks. Both oaks' scaling exponents are higher than findings in savanna ecosystems, and pines higher than those in light-limited forests (Loubota Panzou et al., 2021). Our findings also align with a recent TLS study in the tropics where crown depth was shallower for light demanding and deeper for shade tolerant species (Martin-Ducup et al., 2020). Higher shade tolerance in both oaks facilitates the maintenance of lower branches and therefore more leaf layers with net carbon gain (Niinemets, 2010), whereas both light demanding pines are likely to abscise lower branches to avoid a negative carbon balance (Aiba & Nakashizuka, 2009; Poorter et al., 2012). This pattern may also emerge due to denser wood being more resistant to damage and disease (Loehle, 1988). Shade tolerant species are likely more able to retain, or even increase in the case of *Q. faginea*, crown depth with height, resulting in crowns having many vertical leaf layers (Niinemets, 2010), which may be beneficial in moderating the effects of drought (Domingo et al., 2019) but in direct contradiction with Horn's, (1971) hypothesis. Crown depth was the least systematically variable crown metric across our study site (Table 1), being the only metric to select for models excluding plot as a random effect (Table S2). Competitive effects on crown depth were absent for most species (except *P. nigra*), in contrast to other studies that have found a response to local light availability (Harja et al., 2012; Poorter et al., 2012).

4.5 | Challenges in disentangling different modes of competition

There are many challenges in teasing apart the components of neighbourhood competitive interactions. A recurring issue is the selection of neighbourhood radius to determine which trees are likely imposing competitive pressures on the focal tree (Zambrano et al., 2019). For instance, both 5 m (Grossiord et al., 2014) and 10 m (Gómez-Aparicio et al., 2011) neighbourhoods have been used in Mediterranean forests of Spain, 10 m in temperate forests of British Columbia, Canada (Thorpe et al., 2010), 15 m radius in the French Alps (Kunstler et al., 2012), 25 m in the Southeastern USA (Zhao et al., 2006) and 30 m on Barro Colorado Island (Chen et al., 2016). Alternatively (as we have done here), neighbourhood size can be set to vary according to the dimensions of the focal tree crown (Lorimer, 1983; Pretzsch

& Biber, 2010). As an alternative, Biging and Dobbertin (1992) used crown overtopping to represent asymmetric competition in place of specific distance thresholds. The use of crown overlap has outperformed conventional representations in the tropics in predicting growth and survival (Zambrano et al., 2019). However, its performance in simpler, mono-layered forests where overlap is minimal but sideways shading more common, remains untested.

4.6 | New, high-resolution crown and competition metrics from TLS

The capacity of TLS to capture the full irregularity of tree crown structure means the potential not only for better depictions of crown morphology within existing frameworks, but also to represent three-dimensional shading effects within neighbourhoods in full. This study demonstrates how we can use TLS to accurately characterise crown interactions and avoid geometric assumptions, which likely overstate competition for light (Krůček et al., 2019; Figures S6 and S7). A movement towards more refined light illumination indices (e.g. Canham et al., 2004; Rüger & Condit, 2012) underpinned by highly accurate representations of crown morphology and positioning (Metz et al., 2013) and leaf/wood separated point clouds (Vicari et al., 2019), will lead to more comprehensive analyses of tree to tree interactions informed by explicitly represented shading effects. Novel analyses working with full three-dimensional tree canopy interactions will provide new insights into tree-tree interactions above- and below-ground.

5 | CONCLUSIONS

This study has demonstrated that a wide range of TLS-derived crown metrics scaled below theoretical predictions and were negatively affected by above-ground competition. We found that other factors than optimisation principles were important in determining crown morphology: asymmetric competition was important for pine species and symmetric competition was for oaks. These findings agree with known shade tolerances, with pines showing higher sensitivity to shading and oaks able to tolerate sub-canopy conditions and therefore mostly sensitive to below-ground competition. In contrast to other work in these forests, our novel TLS neighbourhood analyses showed little evidence of the effect of local scale genus diversity on crown morphology, although post-hoc analyses, showed that genus diversity might be influential at the plot scale. We have demonstrated the capacity of TLS to capture two- and three-dimensional crown properties, and to characterise, high-resolution neighbourhood competition metrics not available using traditional techniques. These have allowed us to not only test a prominent ecological scaling theory's assumptions and predictions along with competitive interactions in wholly new ways, but also highlight the further potential of these three-dimensional data to understand forest ecological processes.

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AUTHORS' CONTRIBUTIONS

H.J.F.O. and E.R.L. conceived the ideas and designed the methodology; H.J.F.O. and W.R.M.F. collected and processed the TLS data; H.J.F.O. performed the analysis with support of E.R.L.; H.J.F.O. led the writing of the manuscript with input from W.R.M.F. and E.R.L. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Focal tree crown and neighbourhood metric data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.0k6djhb0m (Owen et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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